

SOCIOECOLOGICAL AND SOIL-PLANT STUDIES OF THE NATURAL VEGETATION IN THE NORTHERN MOJAVE DESERT-GREAT BASIN DESERT INTERFACE

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ABSTRACT.— The purpose of this study is to further describe the distribution, habitats, and ecological characteristics of the natural vegetation in the northern sector of the northern Mojave Desert. Sixty-six stands were classified on the basis of shared leading dominant species. Each of these groupings is well defined and represents a sociologically distinct entity quite recognizable in the field. The relationships between each vegetational grouping and several environmental variables were statistically analyzed. Significant differences were found among plant groupings with respect to soil moisture tension, absolute and relative amounts of exchangeable Na, exchangeable K, cation exchange capacity, and elevation.

The analysis of the relationship between the phytosociological behavior of the major leading dominant species and the environmental variables shows that some of the simple, or multiple, linear correlations obtained with regard to *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. were highly significant. *Atriplex confertifolia* (Torr. & Frem.) S. Wats. and *Atriplex canescens* (Pursh) Nutt. showed the highest number of significant correlations obtained.

Diversity varies from one vegetational grouping to the other as well as between stands of the same grouping. The grouping of *L. tridentata* has proved to be the most widespread, diversified, and, consequently, the most stable vegetation cover in the study area; it, therefore, represents a climax community. The vegetational grouping dominated by *A. confertifolia*, on the other hand, appears not to be a climax community.

The patchiness of the earth's surface in terms of climate, edaphic factors, and physiography extends from large areas to minute areas; that is, the difference may be major, as, for example, between desert and grassland ecosystems, or minor, as between the soil surface under a shrub and the surface a few centimeters away.

The most basic relation between the patchiness of the environment and the forms and distribution of organisms is that of plants. In given climate and soil conditions, certain plant species can survive. In addition, all plants that can survive a particular set of environmental conditions themselves contribute to local climate and microclimatic conditions; all interact to form a characteristic recognizable ecological system.

The relationship between the biotic and abiotic components of a given ecosystem is complicated, and data available that relate the behavior of the whole biotic components to a biotic factor are scarce. This paucity of

data is understandable in view of difficulties involved in collection, particularly when matters are related to such large-scale ecosystems as deserts.

Additional ecological investigations in the northern Mojave Desert areas destined for various exploitations are needed. Many important studies have already been made in the general area (Allred et al. 1963, Beatley 1963, 1969, 1974, 1975, 1976, Wallace and Romney 1972, Romney et al. 1973), but much yet remains to be explained.

Special stress should be laid on the study of the natural vegetation and its synecology, with special attention to soil-vegetation relationships. This paper has an aim of providing a quantitative description of the vegetation and environment for certain sites in the northern sector of the Mojave Desert. It includes an assessment of the relationship between the distributional behavior of some vegetational groupings and local environmental variations.

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Study Area Physiography and Soil Characteristics

The physiography of the study area is described in the above references. Briefly it is characterized by low-lying, sparsely vegetated, rugged mountain ranges and intervening valleys into which the erosional material has been deposited over ages, creating extensive alluvial fanlike deposits. These deposits, extending from the bases of the mountains and hills, comprise the bajadas, or foothills. The composition of the bajadas is reflected in the source from which the erosional material was derived and the degree of incline and deposition.

Another characteristic feature of the northern Mojave Desert is those valleys in which moisture is trapped when runoff occurs from the surrounding terrain. The silt-laden waters, which eventually reach the lowest elevation in such valleys, concentrate as ephemeral bodies which, upon elevation, leave a deposit of fine silt and clay that becomes very hard when dry. These lake beds are termed playas and for the most part lack conspicuous vegetation. These physiographic features of the Mojave Desert are in some respects similar to the Arabian inland deserts in Syria, Jordan, Iraq, and Saudi Arabia.

The principal geographic areas in which the present study was conducted are located in two closed and three open drainage basins, located on the Nevada Test Site in southern Nevada. Two of the five valleys in this area, Frenchman and Yucca valleys, are closed catchment basins in which large playas exist. They, particularly Yucca, represent transition to Great Basin vegetation. The other valleys, generally known as Rock Valley and Jackass Flats and Mercury Valley, are not landlocked basins. They all have transitional Great Basin-Mojave Desert vegetation. They drain to the southwest into the Amargosa drainage system terminating in Death Valley. The northernmost flat in the study is Yucca Flat, south of which is Frenchman Flat, separated from the former by a low ridge called Yucca Pass. The alluvial thickness toward the central part of Yucca Flat is about 250-300 m, and about 200 m in the playa in Frenchman Flat (Allred et al. 1963). Most of the soils in the different study sites are calcareous, but

some are low in lime because of the influence of alluvial materials of volcanic origin.

Climate

The climate of the area is also described in the above references. The study sites lie to the east and leeward side of the Sierra Nevada, which forms a massive barrier to the prevailing winds from the west. This barrier to moist air has resulted, at least in part, in a vast desert region of which the northern Mojave Desert is a part. Annual rainfall averages from 10 to 15 cm, most of which occurs in late winter. Summer rainfall is principally due to convective showers associated with thunderstorms, which in turn are induced by high humidity. This phenomenon results in considerable annual variation in precipitation, with some microgeographical variation within a given year. There is also a pronounced difference in mean annual rainfall. Snowfall is sparse in the lower valleys and usually only present for short winter periods.

The average temperatures vary with the location, from 18 to 25 C, maximum, and 4 to 11 C, minimum. The highest temperature recorded was 44 C in July 1959 at Jackass Flats; the minimum was -16 C in January 1955 at Yucca Flat.

The relative humidity varies from 2 percent to approximately 90 percent, the highest occurring in predawn hours and the lowest during daylight hours. The average is about 21 percent in summer as contrasted with 30 percent in winter.

MATERIALS AND METHODS

Selection of Stands and Vegetation Sampling

To encompass a broad spectrum and diversity of vegetation types, 66 stands were selected along the various environmental gradients encountered in the different study sites. Maps prepared by Beatley (1969) assisted in the selection. The number of stands varied according to the complexity of the vegetation from 27 in Frenchman Flat to 6 in Yucca Flat. In selecting each stand, a reasonable degree of physiognomic and physiographic homogeneity was secured by visual

judgment. Some cogent ecological attributes of perennial vegetation at each stand were determined by nondestructive, dimensional measurements. Procedural details and calculations involving this method have been reported (Wallace and Romney 1972, Romney et al. 1973). Briefly, two 2×25 m quadrats were laid out in undisturbed vegetation at right angles to each other. All perennial plants within each quadrat were identified to the species level and measured for height and width and size (mean of two dimensions). Shrubs with canopies overlapping the quadrat boundary were counted inside only when their root crown was inside the boundary line. Calculations using these dimensional measurements were made for each species to estimate absolute density, cover, and volume. The corresponding relative values for density and cover were then calculated and summed to give a stand-importance value ranging between 0.0 and 200.

Treatment of the Vegetation Data

When a many-species population is sampled, it is interesting to inquire whether the units are naturally classifiable into distinct groups. Pielou (1969) suggested that it was always possible to subdivide a collection of quadrats in one way or another (i.e., classify them), but it does not follow that the vegetation they represent is classifiable into well-defined separate parts. From the theoretical point of view, there are two main concepts concerning the nature of the vegetation: the association concept and the continuum concept. According to the association concept, vegetation is composed of well-defined, discrete, integrated units that can be combined to form abstract associations reflective of natural entities in the real world. According to the continuum concept, on the other hand, vegetation changes continuously and is not differentiated, except arbitrarily, into sociological entities.

In the present study, it was found that a fruitful way to proceed with vegetation study was to apply a simple approach to account for vegetation structure and then evaluate the consequences of this approach by more sophisticated mathematical arguments.

The technique adopted was originally used

by Brown and Curtis (1952) as an approach for expressing the continuum nature of the upland conifer-hardwood forests of northern Wisconsin. More recently Karboush et al. (1975) have applied the same approach for classifying the fungal flora in some parts of the Egyptian desert.

According to this technique, an importance value was calculated for each species in each of the 66 stands examined. By inspection of the importance values, each stand in turn is assigned a leading dominant, i.e., that species with the highest importance value. Stands with the same leading dominant are then grouped. Obviously, some of the subordinate species in any one stand will be the leading dominants of other stands. Average importance values are then calculated for each species in each group of stands. The group of stands (or group of species) with the same leading dominant is conveniently referred to as a vegetational grouping somewhat like the ecological grouping of Whittaker (1967).

Soil Sampling and Analysis

At each stand a trench was dug extending across a representative shrub clump for a given site and out into the bare area between shrub clumps. This was done to permit an examination and sampling soil profile under both shrub and bare areas in order to investigate the modifying influence of perennial vegetation on desert soils. The depth of each trench was to the caliche hardpan, or, if no restricting layer existed, to an arbitrary depth well into the C horizon. Soil samples were taken from each profile horizon under both shrub and bare areas. These samples were screened in the field to pass a 6.3 mm sieve, and the rock and gravel contents were estimated and discarded. The remaining samples were transported to the laboratory, where they were oven dried and then further screened to pass a 2 mm sieve. Available phosphorus was extracted with sodium bicarbonate and determined colorimetrically using the method of Olsen et al. (1954) as described by Chapman and Pratt (1961). Lime content was determined by the manometric method of Williams (1948). The available iron, zinc, copper, and manganese were ex-

tracted with DTPA (diethylene triamine pentaacetic acid) chelate and determined by atomic absorption as described by Lindsay and Norvell (1969). Organic nitrogen analysis was by the Kjeldahl method (Bremner 1965). Analytical methods used to determine other physical and chemical properties were those of the USDA Salinity Laboratory Staff (1954).

In the present paper, unless otherwise mentioned, correlation is made between properties of soils collected under the shrub and plant. Data for all soil profile variables have been adjusted through a computer program to mean values for the 2.5 to 30 cm soil depth.

RESULTS

Spatial Variations in Vegetation Cover

The data from the phytosociological analysis that aim at providing a picture of the general composition of the perennial vegetation of the study areas are given in Table 1. Thirty-five species were encountered. None of these species can be considered as a leading dominant of the whole study area; instead, some exhibit local dominance or are distinctly more important in certain groups of stands. Six major vegetational groupings have been defined (Table 1). The number of stands for each grouping varies between 15 for the most representative species (*L. tridentata*) and 5 for the least (*Grayia spinosa* (Hook.) Moq. and *Acamptopappus shockleyi* A. Gray). Each of the leading dominant species of these groupings, i.e., *L. tridentata*, *Ambrosia dumosa* (A. Gray) Payne, *G. spinosa*, *A. shockleyi*, *Atriplex confertifolia*, and *Atriplex canescens*, attained a maximum stand-importance value of more than 100 out of 200 and an average group-importance value, based on the structure of the stands in each group of that particular species, of more than 66 (Table 1).

Another five vegetational groupings of minor representation have also been identified. Each of the leading dominant species of these groupings, viz., *Coleogyne ramosissima* Torr., *Lycium shockleyi*, *Menodora spinescens* A. Gray, *Ephedra nevadensis* S. Wats., and *Krameria parvifolia* Benth. attained an absolute

maximum importance value of more than 60 and an average value of more than 50. Each of these groupings is represented by a minimum of two stands and a maximum of four.

Some other species, such as *Lepidium fremontii* S. Wats., *Ceratoides lanata* (Pursh) J. T. Howell, *Hymenoclea salsola* Torr. and Gray, *Lycium andersonii* A. Gray, *Psoralea thamnus fremontii* (Torr.) Barneby, *Lycium pallidum* A. Gray, and *Oryzopsis hymenoides* (Roem. & Schult.) Ricker, though important and common species, are not dominant and accordingly are not included in the provisional arrangement of leading dominant species.

An ecotonal grouping has also been identified (Table 1). It includes six stands in which the dominance is shared by two or more species of the nonleading dominants. Thus, almost 10 percent of the stands did not fit into the system.

It is clear from Table 1 that, in the vegetational grouping dominated by *L. tridentata* (I.V. = 87) (I.V. is importance value), the subordinate species are *A. dumosa* (I.V. = 31) followed by *L. andersonii* (I.V. = 17). Other species associated with *L. tridentata* are mostly of minor importance because their average importance values are generally below 10. In the *A. dumosa* grouping (I.V. = 80) the next highest importance value to that of *A. dumosa* is 31 for *L. tridentata* and 15 for *G. spinosa*. Other species of some importance are *K. parvifolia* (I.V. = 12) and *E. nevadensis* (I.V. = 11). In the *G. spinosa* grouping (I.V. = 79), the subordinate species were *L. andersonii* (I.V. = 27) and *L. tridentata* (I.V. = 20). Other important species in this grouping are *A. dumosa* (I.V. = 16) and *E. nevadensis*. In the *A. shockleyi* grouping (I.V. = 66), the species second in importance is *L. tridentata* (I.V. = 31) followed by *G. spinosa* (I.V. = 22), *L. andersonii* (I.V. = 16), and *A. dumosa* (I.V. = 15). *Ceratoides lanata* (I.V. = 13) is also of some significance in this grouping. The vegetational groupings of *A. confertifolia* (I.V. = 129) and *A. canescens* (I.V. = 137) are of some interest. In the first grouping only one species, *L. tridentata*, seems of some importance (I.V. = 25). All other species are of very low importance value and consequently of minor significance in community structure. In the vegetational

grouping, the species second in importance is *A. confertifolia*, but its very low importance value of 13 makes it of minor significance in this grouping. Another point of interest is the relatively very low number of species in these two groupings. In either grouping the number of species does not exceed 10, compared with about 20 in the other vegetational groupings. It is also obvious from Table 1 that *L. tridentata*, which is an integral component of all other vegetational groupings

identified, is missing from the *A. canescens* grouping.

The structure of the vegetational groupings defined as being of minor representation is also given in Table 1. *Larrea tridentata* can be considered as a common species in all groupings. It is, however, particularly well represented in the *M. spinescens* and *A. shockleyi* groupings. Its importance values in these two groupings are 47 and 31, respectively. The high (112) importance value of *C.*

TABLE 1. Average importance values of plant species in provisionally defined vegetational groupings.

SPECIES	VEGETATIONAL GROUPINGS												
	Major						Minor						
	<i>L. trid.</i>	<i>A. dum.</i>	<i>G. spin.</i>	<i>A. shock.</i>	<i>A. conf.</i>	<i>A. can.</i>	<i>C. ram.</i>	<i>L. shock.</i>	<i>M. spin.</i>	<i>E. nev.</i>	<i>K. par.</i>	Eco- total	
A. LEADING DOMINANTS													
<i>Larrea tridentata</i> (15)*	57	31	20	31	25	—	17	31	47	22	19	17	
<i>Ambrosia dumosa</i> (10)	31	80	16	15	4	0.6	0.2	8	3	15	29	18	
<i>Grayia spinosa</i> (5)	10	15	79	22	—	0.5	7.5	—	1.5	—	23	18	
<i>Acanthopappus shockleyi</i> (5)	6	9	8.6	66	2	—	—	21	3.5	—	—	6	
<i>Atriplex confertifolia</i> (6)	5	—	—	—	129	13	—	—	—	—	—	4.4	
<i>Atriplex canescens</i> (6)	3	1	—	—	9	137	3.2	33	2	15	—	—	
<i>Coleogyne ramosissima</i> (4)	—	7	—	—	—	—	112	6	—	—	—	—	
<i>Lycium shockleyi</i> (3)	—	—	—	—	—	—	—	88	—	—	—	—	
<i>Mendora spinescens</i> (2)	3	5	—	—	0.6	—	1.2	5	79	26	—	0.2	
<i>Ephedra nevadensis</i> (2)	5	11	10	5	—	—	16	—	16	73	25	9	
<i>Krameria parvifolia</i> (2)	6	12	—	5	—	—	—	3.6	11	38	54	11	
B. COMMON													
<i>Lepidium fremontii</i> (1)	1	0.2	0.4	0.6	—	—	—	—	—	—	—	17.3	
<i>Ceratoides lanata</i>	5	3.5	9	13	7	7	1.8	—	5	5.5	4.6	23	
<i>Hymenoclea salsola</i>	1	—	4	3	4	4	—	0.3	—	—	—	4	
<i>Lycium andersonii</i>	17	8.7	27	16	—	—	15	—	4	—	32	21	
<i>Dalea fremontii</i>	1	1.4	—	0.1	—	—	0	1.2	—	—	—	25	
<i>Lycium pallidum</i>	3	5	5	3	—	—	—	—	—	—	15	14.4	
<i>Oryzopsis hymenoides</i>	6	9	9	11	2	2	—	2.7	9	5	1.9	6.4	
C. INFREQUENT OR OF MINOR IMPORTANCE													
<i>Sphaeralcea ambigua</i>	3	1.4	—	1.4	0.5	0.5	1.3	1.5	3.5	—	—	1	
<i>Yucca schidigera</i>	4	—	—	1.3	—	—	—	—	—	—	—	—	
<i>Ephedra funerea</i>	1.4	1	—	—	—	—	—	1.5	0.3	—	—	—	
<i>Hilaria rigida</i>	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Stanleya pinnata</i>	—	—	—	—	—	—	—	—	—	—	—	15.8	
<i>Mirabilis pudica</i>	—	—	—	—	—	—	—	0.2	—	—	—	0.3	
<i>Tetradymia axillaris</i>	—	—	1	0.6	—	—	2.2	—	—	—	—	1.2	
<i>Stipa speciosa</i>	—	—	5.2	—	—	—	11	—	—	—	—	1.5	
<i>Artemisia spinescens</i>	—	—	1	—	—	—	—	—	—	—	—	1.1	
<i>Dalea polyadenia</i>	1	—	—	—	—	—	—	—	—	—	—	—	
<i>Cactus sp.</i>	0.7	—	0.1	—	—	—	—	—	0.8	—	—	1.1	
<i>Prunus fasciculata</i>	—	—	—	—	—	—	—	—	—	—	—	0.5	
<i>Salazaria mexicana</i>	—	0.1	—	—	—	—	—	0.9	—	—	—	—	
<i>Yucca brevifolia</i>	1.5	—	—	—	—	—	7.5	0.7	—	—	—	—	
<i>Thamnosma montana</i>	0.2	—	—	—	—	—	—	—	—	—	—	—	
<i>Haplopappus cooperi</i>	—	—	3.1	1.2	—	—	—	—	—	—	—	—	
<i>Machaeranthera tortifolia</i>	—	—	1	—	1	—	—	3	—	—	—	—	

*Number of stands in which the species is the leading dominant.

ings identified. It is clear that similarity coefficients between groupings are generally low. Among the highest coefficients are those between the *L. tridentata* grouping and those of *A. shockleyi* (44), *A. dumosa* (33), and *G. spinosa* (31). The *A. dumosa* grouping also has some relatively high similarity indices with those of *G. spinosa* (34), *A. shockleyi* (33), and *M. spinescens* (32). *Grayia spinosa* grouping has high similarity indices with those of *A. shockleyi* (43) and *K. parvifolia* (33). It is interesting to notice that the lowest similarities obtained are those between the grouping of *A. canescens* and all other groupings.

Distribution of Stands with Leading Dominants among the Different Study Sites

In Table 3, stands are grouped according to leading dominant species and the different sites are investigated, viz., Mercury Valley, Frenchman Flat, Rock Valley, Jackass Flats, and Yucca Flat. The average density of the leading dominant species in each of these sites is also presented. *Larrea tridentata* was dominant in 15 stands, 9 of which were in Frenchman Flat (Table 3). The average density of *L. tridentata* within its stands in this site is 1244 plants/ha. The only site in which *L. tridentata* is not represented by stands in which it is a dominant species is Yucca Flat, although *L. tridentata* does occur in the transitional basin (Beatley 1974).

Ambrosia dumosa, on the other hand, is poorly represented in Frenchman Flat and is not dominant in Yucca Flat. In Jackass Flats, where *A. dumosa* is well represented (4 stands out of 10), its average density is 5875 plants/ha. *Grayia spinosa* is also well represented in Yucca flat with an average density of 5600 plants/ha.

Acanthopappus shockleyi shows its dominance in Mercury Valley (3 stands) and Jackass Flats (2 stands). Its average density in these two sites is 7400 and 6300 plants/ha, respectively.

Atriplex confertifolia and *A. canescens* reach maximum dominance in Frenchman Flat. One stand with *A. confertifolia* as a leading dominant has been reported in Mercury Valley. The average density per hectare for either of the two species (in Frenchman Flat) is about 3400 plants.

Grayia spinosa is mostly represented in Yucca Flat, and *L. shockleyi* is represented only as a leading dominant species in Frenchman Flat. Stands in which *M. spinescens* and *E. nevadensis* are dominants are equally distributed between Frenchman flat and Jackass Flats, but the stands in which *K. parvifolia* is dominant are highly localized.

Soil Characteristics in Relation to Major Vegetational Groupings

Horizontal variations in some of the soil characteristics among different major vegetational groupings are summarized in Table 4.

TABLE 3. Distribution of stands with leading dominant species among the different study sites, and the average absolute density for each species (no. of plants/ha). (No. of stands in which each species is dominant.)

LEADING DOMINANT SPECIES	SITE				
	Mercury Valley	Frenchman Flat	Rock Valley	Jackass Flat	Yucca Flat
<i>Larrea tridentata</i>	3 (1233)*	9 (1244)	2 (1850)	1 (700)	—
<i>Ambrosia dumosa</i>	3 (3962)	1 (4800)	2 (4400)	4 (5875)	—
<i>Grayia spinosa</i>	1 (3500)	1 (3900)	1 (4800)	—	2 (5600)
<i>Acanthopappus shockleyi</i>	3 (7400)	—	—	2 (6300)	—
<i>Atriplex confertifolia</i>	1 (2900)	4 (3370)	—	—	—
<i>Atriplex canescens</i>	—	6 (3430)	—	—	—
<i>Coleogyne ramosissima</i>	—	—	—	1 (14100)	3 (5370)
<i>Lycium shockleyi</i>	—	3 (5130)	—	—	—
<i>Menodora spinescens</i>	—	1 (7700)	—	1 (4400)	—
<i>Ephedra nevadensis</i>	—	1 (3300)	—	1 (600)	—
<i>Krameria parvifolia</i>	—	—	2 (2500)	—	—

*Number between parentheses indicates average density (plants/ha).

A general idea about the magnitude of variation in each of these soil variables can be gained if the average and range are examined. A more precise judgment, however, may be achieved by examining the results of analysis of variance given in Table 5. In this

table the ordered means of soil variables that show significant variations among major vegetational groupings are presented. Six soil variables out of 16 (given in Table 4) show significant variations: soil moisture retention capacity at 0.0 bar, exchangeable Na, ex-

TABLE 4. Average and range of soil variables in different major vegetational groupings (for statistical difference see Table 5).

SOIL VARIABLE	VEGETATIONAL GROUPINGS					
	<i>L. tridentata</i>	<i>A. dumosa</i>	<i>G. spinosa</i>	<i>A. shockleyi</i>	<i>A. confertifolia</i>	<i>A. canescens</i>
Soil moisture retention at 0.0 bar	12.7 7.6-20.6	9.7 4.8-16.0	12.4 8.8-17.8	12.5 5.1-18.9	13.5 10.4-17.0	19.3 8.8-33.5
pH	8.64 8.3-8.8	8.5 7.8-8.8	8.5 8.4-8.7	8.3 8.4-8.8	8.66 8.3-8.9	8.65 8.5-8.8
E.C. mmhos/cm	1.84 1.0-3.3	1.17 0.39-2.5	1.65 1.2-2.6	1.15 1.1-2.6	1.45 0.3-3.0	1.88 0.55-3.2
Lime %	13.3 0.9-30	6.0 0.1-14.3	8.1 1.0-22.9	10.0 0.2-20.7	12.5 5.7-24.4	13.8 2.4-30
Ex. Na ⁺ meq/100 gm	0.41 0.2-1.0	0.33 0.22-0.6	0.41 0.2-0.73	0.42 0.3-0.53	2.22 0.2-0.4	0.55 0.4-0.8
Ex. K ⁺ meq/100 gm	4.47 2.5-8.1	3.38 2.1-5.6	4.66 2.8-8.7	2.89 2.6-3.6	7.56 3.2-13.5	5.66 0.9-9.1
Ex. Ca ⁺⁺ + Mg ⁺⁺ meq /100 gm	7.86 4.1-11.8	7.52 2.6-13.4	9.11 7.4-11.3	8.72 3.5-12.9	9.08 2.6-18.0	7.31 5.7-10.9
Ex. Na ⁺ %	3.39 1.7-8.4	3.18 1.5-7.6	4.76 1.7-3.8	3.68 2.5-5.6	12.1 2.6-22.1	3.42 1.9-6.2
Cat. Ex. Cap. meq/100 gm	12.8 9.5-15.8	11.3 6-17	14.2 11.2-18.8	12.4 6.9-16.0	15.3 8.4-19.3	17.2 12.6-22.5
(NaHCO ₃) phosphorus ppm	1.88 0.2-4.3	1.56 0.5-3.3	2.2 1.1-5.7	1.8 0.7-3.4	0.52 0.2-1.2	1.5 0.8-2.3
(DTPA) Iron ppm	0.33 0.1-0.7	0.31 .02-0.6	0.33 0.3-0.6	0.38 0.2-0.5	0.16 0.1-0.3	0.23 0.1-0.3
(DTPA) Zinc ppm	0.67 0.3-1.33	0.46 0.2-0.67	0.52 0.31-0.8	0.6 0.3-1.3	0.51 0.3-0.7	9.44 0.16-0.73
(DTPA) Copper ppm	0.13 0.1-0.22	0.126 0.05-0.2	0.23 0.13-0.45	0.15 0.1-0.26	0.16 0.1-0.2	0.22 0.1-0.27
(DTPA) Manganese ppm	2.58 1.2-3.8	2.51 0.9-5.1	2.6 1.6-3.8	3.0 1.3-6.1	1.96 1.2-3.0	2 1.0-2.55
Org. nitrogen %	0.07 0.04-0.095	0.062 0.026-0.12	0.07 0.04-0.1	0.09 0.02-0.13	0.03 0.02-0.04	0.06 0.03-0.08
Elevation m	1030 960-1134	1007 910-1085	1199 991-1463	1070 1037-1104	997 939-1207	955 945-979

changeable K, exchangeable Na expressed as percentage of the total cations, cation exchange capacity, and elevation. The vegetational grouping of *A. dumosa* occupies the stands with the lowest level of soil moisture retention. Groupings of *A. canescens*, on the other hand, occupy stands with the highest moisture retention. Other groupings occupy intermediate positions along the soil moisture retention gradient. Along the exchangeable sodium gradient, the grouping of *A. confertifolia* occupies a significantly high position. The response of the different vegetational groupings to exchangeable K is rather significant. The two groupings of *A. shockleyi* and *A. dumosa* occupy the lower end of the gradient; *A. canescens* occupies the highest portion, and the other groupings are of intermediate positions. In exchangeable Na, expressed as percentage of the total cations, the grouping of *A. confertifolia* occupies soils having the highest levels. It is of interest to notice that the grouping of *A. canescens* occupies an intermediate position along the sodium percent gradient. On the other hand, when we consider the gradient of the total cation exchange capacity, we find that the grouping of *A. canescens* occupies the highest level. *Atriplex canescens* does populate low-lying areas that have accumulated clay and silt. The distribution of the different vegetational groupings along the elevation gradient presents another point of interest.

There is a stepwise segregation of groupings with altitudinal zonation. The grouping of *A. canescens* occupies the lower level of the gradient, and *G. spinosa* occupies the highest level.

Behavior of Leading Dominant Species along an Environmental Gradient

According to Dagnelle (1965), correlation of species with particular environmental variables has much potential as a tool for explanation of plant distribution though, as always with correlation or regression studies based on observational data, conclusions regarding causation must be hedged with reservation. In this case, the reservations are most likely to concern doubts whether the environmental variable studied is directly responsible or whether it is merely associated with the variable to which the effect observed should be properly ascribed.

In the present study the simple linear correlation between the soil variables and both the importance values and the absolute densities (abundance) for the six major leading dominant species has been calculated (Table 6). The number of significant correlations obtained are very few for most of the species. The results are to be interpreted with caution. The importance value of *L. tridentata* shows one positive correlation ($P < 0.05$) with electrical conductivity (E.C.). This correla-

TABLE 5. Ordered means for soil parameters that showed significant variations among different major vegetational groupings, according to the analysis of variance for unequal cell sizes.

SOIL VARIABLES	9.7 (Ad)	12.4 (Gs)	12.5 (As)	12.7 (Lt)	13.5 (Ao)	19.4 (Ac) ^o
Soil moisture retention						
Ex. Na ⁺ meq/100 gm	0.33 (Ad)	0.41 (La)	0.41 (Gs)	0.42 (As)	0.55 (Ac)	2.22 (Ao)
Ex. K ⁺ meq/100 gm	2.87 (As)	3.38 (Ad)	4.47 (La)	4.66 (Gs)	5.66 (Ao)	7.56 (Ac)
Ex. Na ⁺ %	3.18 (Ad)	3.39 (Ld)	3.42 (Ac)	3.68 (As)	4.76 (Gs)	12.1 (Ao)
Cation ex. cap. meq/100 gm	11.3 (Ad)	12.4 (As)	12.8 (La)	14.2 (Gs)	15.3 (Ao)	17.2 (Ac)
Elevation m	955 (Ac)	977 (Ao)	1007 (Ad)	1030 (Ld)	1070 (As)	1199 (Gs)

^oThe means parenthased are not different from each other; those over different parentheses are. La = *Larrea tridentata*, Ad = *Ambrosia dumosa*, Gs = *Gutierrezia spinosa*, As = *Acamptopappus shockleyi*, Ao = *Atriplex confertifolia*, Ac = *Atriplex canescens*.

tion, however, does not necessarily mean that *L. tridentata* is really increasing its abundance with the progressive increase in E.C. Examining the correlation of the absolute density of the same species with the same soil

variable shows that there is no significant correlation and that the trend of correlation present is even negative. Accordingly, the positive correlation of the importance value of *L. tridentata* with E.C. is actually due to

TABLE 6. Simple correlation coefficients (r) between the importance value (a) and the absolute density (b) of major leading dominant species and soil variables. A single asterisk denotes a significant correlation at the 5 percent probability level, and double, triple, and quadruple asterisks denote a highly significant correlation at the 2, 1, and 0.1 percent probability levels.

SOIL VARIABLE		SPECIES					
		<i>L. tridentata</i>	<i>A. dumosa</i>	<i>C. spinosa</i>	<i>A. shockleyi</i>	<i>A. confertifolia</i>	<i>A. canescens</i>
Soil moisture retention at 0.0 bar	a	-0.036	-0.34**	0.11	0.01	-0.16	0.61*
	b	0.223	-0.39***	-0.18	0.01	0.16	0.91****
pH	a	0.19	-0.15	-0.03	-0.41**	0.05	0.31
	b	-0.10	-0.17	-0.16	-0.16	-0.07	0.18
E.C. mmhos cm	a	0.326*	-0.20	0.23	0.03	0.5**	0.23
	b	-0.071	-0.21	-0.14	0.02	0.15	-0.12
Lime %	a	0.078	-0.27	-0.18	-0.09	-0.25	0.58*
	b	0.22	-0.33*	-0.15	-0.03	-0.10	0.91****
Ex. Na meq/100 g	a	-0.245	-0.31*	-0.17	-0.17	0.45**	-0.35
	b	-0.09	-0.28	-0.10	-0.15	0.63***	-0.31
Ex. K meq/100 g	a	0.226	-0.19	-0.002	-0.21	0.23	-0.01
	b	-0.027	-0.19	-0.05	-0.23	-0.10	-0.39
Ex. Ca + Mg meq/100 g	a	-0.17	-0.11	0.08	0.06	0.40	0.45
	b	-0.06	-0.06	-0.004	0.07	0.13	0.78**
Ex. Na+ %	a	-0.27	-0.31*	-0.21	-0.05	0.49**	-0.4
	b	-0.089	-0.27	-0.14	-0.06	0.56***	-0.44
Cat Exc Cap meq/100 g	a	0.24	-0.12	0.03	-0.15	0.1	0.32
	b	0.04	-0.13	0.01	-0.15	0.35	0.38
(NaHCO ₃) P ppm	a	0.20	-0.01	0.16	0.19	-0.35	0.02
	b	0.14	-0.02	0.10	0.23	-0.60***	-0.06
(DTPA) Fe	a	-0.21	-0.14	0.14	0.19	-0.40	0.5*
	b	-0.10	-0.02	0.31	0.21	-0.053**	0.43
Zn	a	0.004	-0.33*	-0.17	0.13	-0.16	-0.26
	b	0.009	-0.35**	-0.11	0.17	0.08	-0.31
Cu	a	-0.02	-0.15	0.39**	0.06	0.16	0.58*
	b	-0.21	-0.22	0.33*	0.07	0.09	0.55**
Mn	a	0.02	-0.06	0.04	0.33	0.07	0.06
	b	0.03	-0.03	0.09	0.4**	0.31	0.34
Total N %	a	0.09	-0.19	0.02	0.35*	-0.31	0.69**
	b	0.10	0.02	0.04	0.36*	-0.49*	0.51
Elevation m	a	-0.1	-0.28	0.8	0.17	-0.18	-0.68**
	b	-0.2	-0.14	0.39**	0.20	0.05	-0.7***

the decrease in the abundance of its associated species. In fact, all species, including *L. tridentata*, are decreasing their abundance along the E.C. gradient, but *L. tridentata* has the slowest rate.

The correlation between *A. dumosa* and exchangeable Na shows similar results. On the other hand, the abundance of *A. dumosa* shows decidedly significant correlation (negative) with soil moisture retention ($r = -0.39$; $P < 0.01$) and lime ($r = -0.31$; $P < 0.02$). However, the coefficient of determination (r^2) is actually a very low percentage. The abundance and the importance value of *G. spinosa* are positively correlated with copper at 2 percent and 5 percent levels of significance for the two parameters, respectively. The abundance of *G. spinosa* is also positively correlated with altitude ($r = 0.39$; $P < 0.02$). The importance value and abundance of *A. shockleyi* are correlated negatively with pH and positively with total nitrogen, but most of these correlations are at the 5 percent level of significance. The abundance of this species shows also a positive correlation with extractable Cu at the 2 percent level of significance. The highest number of significant correlations obtained are those between *Atriplex* species and the abiotic variables. The abundance of *A. confertifolia* shows positive correlations with both absolute and relative amounts of exchangeable Na at the 0.1 percent level of significance. On the other hand, it shows negative correlations with phosphorus ($P < 0.01$), iron ($P < 0.02$), and total nitrogen ($P < 0.05$). The importance values of *A. confertifolia* show only two positive correlations with both absolute and relative amounts of exchangeable Na at the 5 percent and 1 percent levels of significance. *Atriplex canescens* behaves in a different manner; it shows no correlation with any of the soil variables associated with *A. confertifolia* (Table 6). Four soil variables, namely, soil moisture retention, lime, exchangeable Ca + Mg, and Cu show strong positive correlations with the abundance of *A. canescens*. The high values for the coefficient of determination (r^2) of 0.83 for soil moisture, 0.3 for lime, 0.63 for Ca + Mg, and 0.42 for Cu indicate the significance of the role of these soil variables in affecting the distribution and abundance of *A. canescens*. The negative correlation of the

same species with altitude is also highly significant. This may be related to drainage in that the species does occur at the bottom of drainage basins. The importance value of *A. canescens* also shows positive correlations (but mostly at low significance) with soil moisture retention, lime, copper, and total nitrogen.

The multiple linear correlations (R) relating the abundance of the different leading dominant species and the different combinations of soil variables are given in Table 7. *Atriplex confertifolia*, *A. canescens*, and *A. shockleyi* show the greatest number and the highest magnitude of significant relationships with the different combinations of soil variables. *Larrea tridentata*, *A. dumosa*, and *G. spinosa* show smaller numbers of significant correlations.

The following are multiple regression equations relating the absolute density (number of plants/ha of the three species highly correlated with the different combinations of environmental variables: (for the level of significance see Table 7).

A) *Atriplex canescens*

$$\text{Absolute density} = 1.04 \text{ moisture retention \%} + 1.0 \text{ lime \%} - 2.72 \quad (R=0.9^{*****})$$

$$\text{Absolute density} = 51.3 - 5.5 \text{ pH} + 1.92 \text{ lime \%} \quad (R=-0.92^{*****})$$

$$\text{Absolute density} = 0.19 - 3.1 \text{ Na \%} + 0.26 \text{ K \%} + 3.32 \text{ (Ca+Mg)\%} \quad (R=0.82^{*****})$$

$$\text{Absolute density} = 15.3 + 58.2 \text{ Fe ppm} - 26.7 \text{ Zn ppm} + 148.4 \text{ Cu ppm} - 6.7 \text{ Mn ppm} \quad (R=0.72^{***})$$

B) *Atriplex confertifolia*

$$\text{Absolute density} = 10.1 \text{ pH} - 10.5 \text{ P \%} - 199 \text{ N \%} - 50.1 \quad (R=0.7^{***})$$

$$\text{Absolute density} = 9.53 \text{ Na \%} - 0.7 \text{ K \%} + 1.05 \text{ (Ca+Mg)\%} - 0.157 \quad (R=0.7^{***})$$

C) *Acamptopappus shockleyi*

$$\text{Absolute density} = 365.7 - 34.3 \text{ pH} + 1.6 \text{ P \%} + 359.6 \text{ N \%} \quad (R=0.6^{*****})$$

Diversity in
Different Vegetational Groupings

The various ways of defining and measuring diversity have been reviewed and dis-

cussed by Pielou (1969). According to Pielou's definition, diversity is a single statistic in which the number of species and the evenness (uniform distribution of individuals among species) are combined. A collection is said to have high diversity if it has many species and their abundance is fairly even. Conversely, diversity is low when the species are few and their abundance uneven. It should be noted, however, that diversity is sometimes used as a synonym for a number of species; that is not the sense in which it is used here.

In the present study, the Simpson's (1949) measure of diversity as quoted by Pielou (1969) has been used for calculating the diversity in the different major vegetational groupings. This index reads as follows:

$$D = 1 - \frac{1}{N(N-1)} \sum_j N_j(N_j-1)$$

where D is Simpson's measure of diversity in an S species collection containing N individuals, of which N_j belongs to the jth species

$$(j = 1, 2, 3, \dots, S; \sum_j N_j = N)$$

The results of this study are given in Table 8. The vegetational groupings studied can be classified into two main categories. The first category is characterized by low diversity (<0.4) as well as by a wide range of variation. This category includes the vegetational groupings of *A. confertifolia* and *A. canescens*. In one of the stands of *A. confertifolia* the whole population is *A. confertifolia* with a consequent zero diversity. The second category includes the groupings *L. tridentata*, *A.*

dumosa, *G. spinosa*, and *A. shockleyi*. The diversity in these groupings is fairly high (>0.7) and with a narrow variation range. These results obviously indicate the poverty in species and unevenness in the distribution of individuals among species in stands representative of the vegetational groupings of the first category. Conversely, there are a richness in species and an evenness in individual distribution in stands representative of the vegetational groupings in the second category.

DISCUSSION

Since climatic, topographic, edaphic, and biotic conditions vary to a greater or lesser degree within a landscape, numerous habitats and plant communities are formed and become manifest in a mosaic or zonation of vegetation. An important feature of vegetation, therefore, is change. The causal factor or factors behind this change is of primary concern to biologists, soil scientists, and even to geologists.

Environmental variations generally occur in the form of gradients on different scales. Some of those gradients are described as microgradients (Hanson and Churchill 1965). They may be caused by soil variations in microrelief, texture, organic content, phosphorus content, or any other conditions that might be of direct or indirect influence on plant life and existence. The soil sampling program was not intensive enough to reflect all these.

TABLE 7. Multiple correlation (R) between the absolute density of each of six leading dominant species and variations in multiple combination of soil variables. A single asterisk denotes a significant correlation at the 5 percent probability level, and double, triple, and quadruple asterisks denote high significant correlation at 2, 1, and 0.1 percent probability levels.

COMBINED SOIL VARIABLES	SPECIES					
	<i>L.</i> <i>tridentata</i>	<i>A.</i> <i>dumosa</i>	<i>G.</i> <i>spinosa</i>	<i>A.</i> <i>shockleyi</i>	<i>A.</i> <i>canescens</i>	<i>A.</i> <i>confertifolia</i>
All variables	0.51****	0.67****	0.74****	0.93****	1.0****	0.95****
Fe, Zn, Cu, Mn	0.37**	0.31	0.42**	0.49**	0.72***	0.62***
pH, P, N	0.19	0.30°	0.18	0.60****	0.67**	0.70****
Na, K, Ca + Mn	0.15	0.27	0.16	0.23	0.82****	0.7****
E.C., Na%, Cat. ex. cap	0.11	0.31°	0.2	0.18	0.64**	0.6***
Moisture, lime	0.32*	0.34°	0.18	0.05	0.93****	0.29
pH, lime	0.28	0.38**	0.15	0.39*	0.92****	0.09
pH, P	0.18	0.17	0.18	0.44**	0.11	0.63***

The behavior of the biotic communities in the Mojave Desert in general or in some of its sectors has attracted the attention of many biologists. Shreve and Wiggins (1964) have described the Mojave Desert as showing its most distinctive development between 600 and 1200 m elevation (2000–4000 ft). When it is followed thence toward the northeast or southeast, it loses some of its characteristic vegetational features and much of its distinctive flora. The basic structure of the vegetation throughout the Mojave Desert is very open stands of *L. tridentata* and *A. dumosa*. On the western edge these plants are joined and, to some extent, replaced by *Artemisia* sp., *G. spinosa*, *Tetradymia*, and some suffrutescent perennials, and at higher elevations on the north *C. ramosissima* and *G. spinosa* are dominant.

In the northern sector of the Mojave Desert, particularly in the Nevada Test Site and its surroundings, detailed phytosociological and autoecological studies have been carried out by many authors. Among them are Beatley (1963, 1969, 1974, 1975), Allred et al. (1963), Rickard and Beatley (1965), Brown and Mason (1968), and Wallace and Romney (1972). In these studies some vegetational units have been defined and named by various terms as associations, types, and subtypes. The correlation between these vegetational units and certain environmental variables has been discussed also.

In the present study it has proved useful to segregate the stands into several vegetational groupings according to leading dominant species (species with the highest importance values). However, these groupings are not absolutely discrete. The members of each pair of groupings are, in various degrees, linked together by having one or more of the dominant species in common. This, however, does not preclude the fact that these vegetational groupings are well defined and represent so-

biologically distinct entities quite recognizable in the field. Six major and five minor vegetational groupings have been defined. In a wider ecological study these minor groupings may prove to be of major importance.

Several edaphic factors were analyzed statistically in relation to the distribution of each of the major vegetation types. Significant differences were found among the plant groupings with respect to soil moisture tension, absolute and relative amounts of exchangeable Na, exchangeable K, cation exchange capacity, and elevation. However, no one grouping is restricted in its distribution by a narrow tolerance range for any specific soil factor. Overlapping of the vegetational groupings occurred for all the soil variables measured. This overlapping, however, does not preclude the fact that, within the overall structure of the vegetation dealt with, each vegetational grouping studied has a significant association with a particular combination of environmental variables.

The analysis of the relationship between the phytosociological behavior of the major leading dominant species and the environmental variables studied is of certain interest. Only one of the simple linear correlations between the relative or absolute abundance of *L. tridentata* and any of the environmental variables is highly significant. This might be explained by the fact that *L. tridentata* may be so well adapted to the conditions in the study area that its behavior is not noticeably affected by the changes within the limits of any of the factors studied. Other factors could be more important. The coefficient of determination (r^2) of 0.25, as determined from the multiple correlation analysis, indicates that only 25 percent of the total variation in abundance of *L. tridentata* along its range of distribution in the study area is due to the combined effect of the different environmental variables investigated.

TABLE 8. Simpson's measure of diversity in different vegetational groupings.

DIVERSITY	VEGETATIONAL GROUPING					
	<i>L. tridentata</i>	<i>A. dumosa</i>	<i>G. spinosa</i>	<i>A. shockleyi</i>	<i>A. canescens</i>	<i>A. confertifolia</i>
Mean	0.75	0.725	0.706	0.703	0.390	0.33
Range	0.61–0.84	0.64–0.84	0.7–0.8	0.64–0.81	0.18–0.55	0.0–0.73
S.D.	± 0.067	± 0.05	± 0.048	± 0.075	± 0.206	± 0.34
S.E.	± 0.017	± 0.0175	± 0.0214	± 0.034	± 0.08	± 0.155

That *L. tridentata* has a very wide range of distribution has been discussed by many authors. As reviewed by Barbour (1968), it dominates a desert area of 358,000 km² in the southwestern United States; occurs in 183,000 km² in adjacent vegetation; and covers a range that differs widely in climates, soils, elevations, and communities. However, within this distribution range, *L. tridentata* is so ubiquitous that Benson and Darrow (1954) have used its range limits to define the boundaries of the warm desert. More recently Beatley (1974) has suggested that the prevailing low minimum air temperatures and their extremes in the lowlands of drainage basins of Nevada are inferred to be the primary cause of the absence of *L. tridentata* in three discrete vegetation zones. Wallace and Romney (1972) have suggested that the lack of *L. tridentata* in dry lake areas of closed basins in southern Nevada is due to periodic flooding. This species is sensitive to poor root aeration (Lunt et al. 1973).

The analysis of correlation between species behavior and site variables also shows that the concentration of the different ions has a significant role in determining the abundance of some of the different species studied. On the other hand, total salinity as reflected by electrical conductivity or as total soluble cations is of limited significance as a controlling factor. Similar results are obtained by Gates et al. (1956) and Ayyad and El-Ghareeb (1972). In a study on some of the alkali desert soils in Utah, Gates et al. (1956) concluded that total salinity is not a wholly satisfactory criterion and that future work should involve specific ions. Chapman (1960) concluded that the roles of the cations and anions or their combination in relation to vegetation zonation may have far greater importance than has previously been suggested.

On the basis of subjective and qualitative argument, it was for many years believed by the majority of ecologists (Odum 1959, Hanson and Churchill 1965, Pielou 1975) that the more complex a community (that is, the more numerous its species and the more intricate their relationships), the greater the community's system stability would be; for, if each species would rely on many rather than few food sources and be regulated by many rather than few predators, the eggs-in-basket effect

would be minimized. As a result, a high diversity would cause a high community stability.

However, acceptance of this theory has wavered since May (1973) pointed out that community stability is not a mathematical consequence of high species diversity and that the contrary is true. May's theory is still, so far, in its infancy, is a matter of controversy, and may not apply to deserts. As Pielou (1975) suggests, many species models that make no allowance for certain vegetational parameters, such as spatial heterogeneity, are totally unrealistic.

In the present study, the relative stages of community stability for the different vegetational groupings has been discussed on the basis of the assumption that community stability and high diversity are positively correlated (Pielou 1975). It is also based on the assumption that the diversity of an abstract community should be expressed as an average of the diversity measures for the different concrete units of that particular community, and consequently the lower the standard error of the diversity measure, the greater the homogeneity of the community. The vegetational grouping of *L. tridentata*, showing both high diversity and greater homogeneity, may be considered, therefore, as the most stable community in the study area, consequently representing its climatic climax vegetational cover. The vegetational grouping of *A. dumosa* is also characterized by both high diversity and homogeneity, but it has a relatively narrower distribution range.

The view that the *L. tridentata* grouping represents the most stable community in the study area has been supported by the study of Beatley (1969), who described the *L. tridentata* type as the one with the highest floristic diversity in the region, and by Shelford (1963), who described the *L. tridentata* community as representing the bush desert climax. However, the position of the *L. tridentata* community along the successional ladder is a matter of great controversy, and views vary according to phytogeographical regions. According to Stebbins and Major (1965), *L. tridentata* has been described in the Mojave Desert as representing a relict species. On the other hand, in Sampson Valley in southeastern Arizona, Chew and Chew (1965)

have described *L. tridentata* as a pioneer species that has been recently dispersed in the study area at the expense of *Flourensia*. Gardner (1951) concluded also that *L. tridentata* is expanding its distribution and dominance into areas occupied by *Flourensia* in the Rio Grande Valley, New Mexico, probably as the result of changes in the complex of soil factors, especially the loss of surface soil.

ACKNOWLEDGMENTS

This study was supported by Contract EY-76-C-03-1200 between the U.S. Department of Energy and the University of California, CETO of the Nevada Test Site, and the U.S. International Desert Biome Program.

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